



Firth, J., Cole, E., Ioannou, C., Quinn, J. L., Aplin, L. M., Culina, A., McMahon, K., & Sheldon, B. (2018). Personality shapes pair bonding in a wild bird social system. *Nature Ecology and Evolution*, 2(11), 1696–1699. <https://doi.org/10.1038/s41559-018-0670-8>

Peer reviewed version

Link to published version (if available):  
[10.1038/s41559-018-0670-8](https://doi.org/10.1038/s41559-018-0670-8)

[Link to publication record in Explore Bristol Research](#)  
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Springer Nature at <https://www.nature.com/articles/s41559-018-0670-8> . Please refer to any applicable terms of use of the publisher.

## University of Bristol - Explore Bristol Research

### General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:  
<http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

# Personality shapes pair bonding in a wild bird social system

Josh A. Firth<sup>1,2\*</sup>, Ella F. Cole<sup>1</sup>, Christos C. Ioannou<sup>3</sup>, John L. Quinn<sup>4</sup>, Lucy M. Aplin<sup>1,5</sup>, Antica Culina<sup>1,6</sup>, Keith McMahon<sup>1</sup>, Ben C. Sheldon<sup>1</sup>

<sup>1</sup>Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

<sup>2</sup>Merton College, Merton Street, University of Oxford, Oxford, OX1 4JD

<sup>3</sup>School of Biological Sciences, University of Bristol, Bristol, BS81TQ

<sup>4</sup>School of Biological, Earth and Environmental Sciences, University College Cork, North Mall, Cork, Ireland

<sup>5</sup>Max Planck Institute for Ornithology, Radolfzell, Germany

<sup>6</sup>Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, Netherlands

\*Correspondence: Dr. Josh A. Firth [joshua.firth@zoo.ox.ac.uk](mailto:joshua.firth@zoo.ox.ac.uk)

## Three Sentence Abstract

Mated pair bonds are integral to many animal societies, yet how individual variation in behaviour influences their formation remains largely unknown. In a population of wild great tits (*Parus major*), we show that personality shapes pair-bonding: proactive males formed stronger pre-breeding pair-bonds by meeting their future partners sooner and increasing their relationship strength at a faster rate and, as a result, sampled fewer potential mates. Thus, personality may have important implications for social relationship dynamics and emergent social structure.

## Main Text

Pair bonding – the formation of social relationships between mating partners – has evolved across diverse lineages ranging from simple invertebrate social systems to highly complex human societies<sup>1,2</sup>. Pair bonds vary in form across the animal kingdom, from relatively ephemeral associations to life-long monogamous bonds, and shape various ecological processes, such as sexual selection, kinship and social structure, and gene flow<sup>2-5</sup>. Individuals may depend either partly (e.g. humans) or wholly (e.g. truly monogamous bird species) on forming these bonds for reproduction, not only for initial matings, but for a diverse range of activities related to subsequent fitness, such as securing breeding locations, or providing resources to produce or raise offspring<sup>2,6,7</sup>.

While social relationships, such as pair bonds, are a dyadic property, inevitably the evolution of the formation of such relationships arises through individual level processes. Recent research into the genetic and neurobiological proximate mechanisms and ecological consequences of pair-bonds has generated widespread and renewed interest in this topic<sup>8-11</sup>. Yet, how individual-level behavioural variation drives the formation and development of these dyadic relationships remains largely unknown.

Birds provide a model system for investigating pair-bond formation as ~90% of avian species form socially monogamous mated pairs<sup>7,12</sup>, and variation in the duration of the pair-bond appears to be related to reproductive output in various species<sup>13-15</sup>. Birds have also been central in advancing the understanding of repeatable individual behavioural differences (termed 'animal personality') in natural populations<sup>16-18</sup>. In many species, variation in individuals' personalities along measures of the 'reactive to proactive' spectrum is known to be consistent across time and contexts, heritable, related to fitness, and linked to various ecologically relevant behaviours, including social interactions<sup>17,19-29</sup>. Nevertheless, the link between personality and pair-bond dynamics in wild animals remains entirely unexplored. This is likely due to the difficulty of quantifying pair-bond formation (which can often take place over prolonged periods before reproduction<sup>7,30</sup>) amongst individuals with known personalities, and simultaneous monitoring the social system to enable separation of an individual's affiliation to their future partner from their general patterns of social activity.

Here, we examine how individual behavioural characteristics shape pair-bonding dynamics by monitoring social associations occurring during the pre-mating winter period (December to March), over three consecutive years, between wild foraging great tits (*Parus major*) of known personality (quantified on a continuous scale using an activity-exploration assay<sup>16,22</sup> - see *Methods*). Importantly, deriving the social network amongst all dyads each year (winter 2011/12=1085 individuals, 2012/13=720, 2013/14=805 – Supplementary Table 1) enabled us to quantify social associations between individuals and their future breeding partner in relation to their associations with all other birds. By doing so, we could quantify their relative pair-bond strength given their sociability in terms of their propensity to associate with others in general (Fig. 1a).

Considering instances of birds with known personalities in new breeding pairs, of which both members were recorded in the prior winter social network (n=122, 62 males, 60 females), males scored as more proactive held stronger relative social affiliation to their future breeding partners over winter than more reactive males (Linear Mixed Model (LMM) with network randomization procedure controlling for network structure and non-independence: Estimate=0.250±0.105,  $t=2.373$ ,  $p=0.021$ ,  $p_{\text{rand}}=0.040$ , see *Methods* and *Supplementary Information* for full model and randomization details throughout). Females' personality, however, was unrelated to their relative pair-bond strength (Fig. 1b; Supplementary Figure 2).

Due to the large-scale spatiotemporal monitoring of the pre-breeding social associations, it was possible to examine the mechanisms underlying proactive

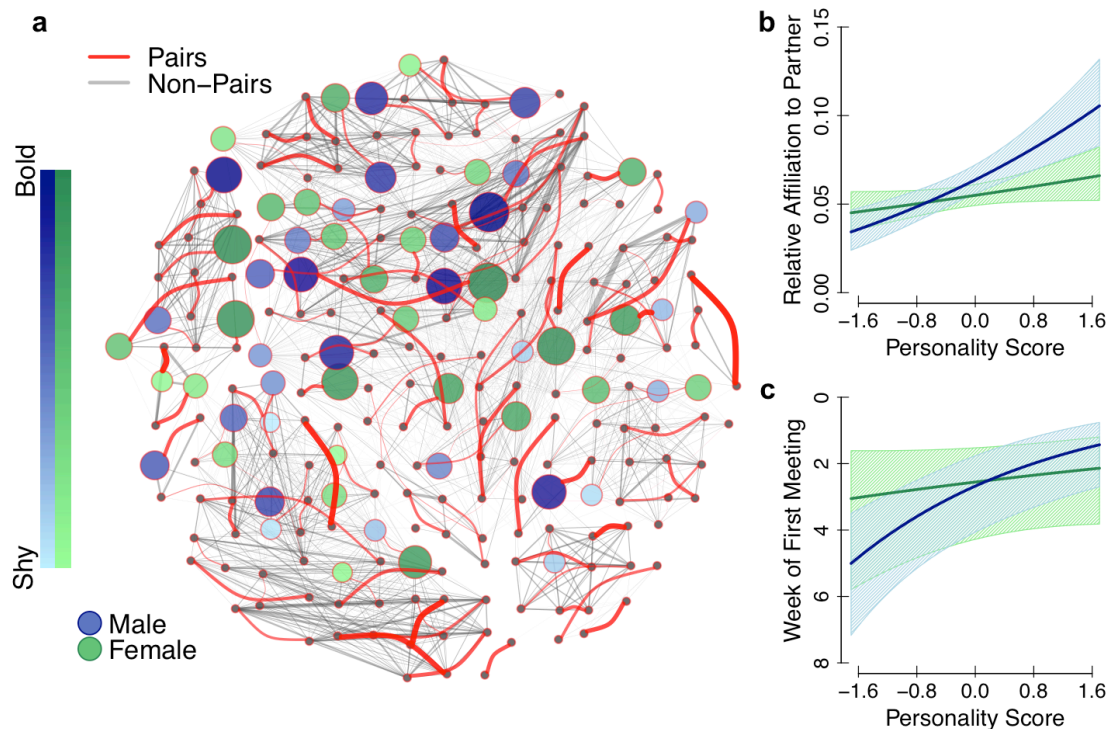
90 males' stronger relative affiliations to their future partners. We found no  
91 evidence that either sex's personality was related to the spatial activity overlap  
92 in a pair's winter range (see *Supplementary information*). However, more  
93 proactive males initially met their future partners sooner as they were observed  
94 in the same flock as their partner earlier in the winter than more reactive males  
95 (Fig. 1c; Generalized Linear Mixed Model: Estimate=-0.368±0.177,  $z=-2.076$ ,  
96  $p=0.038$ ; Also see Supplementary Figure 3).

97  
98 Dynamic social networks, created separately for each sampling period (i.e. each  
99 weekend) throughout each winter, showed that proactive males increased their  
100 relative affiliation to their future partner at a faster rate than reactive males did  
101 (Fig 2a; Supplementary Figure 5a). Week-by-week pair-bond strength was  
102 significantly predicted by the interaction between the male's personality and the  
103 time since they first met their future partner (LMM: Estimate= 0.026±0.009,  
104  $t=2.688$ ,  $p=0.007$ ,  $p_{\text{rand}}=0.008$ ). While females generally showed an increase in  
105 their relative pair bond strength with increased time since first meeting their  
106 partner, this again was not related to their personality (Supplementary Figures  
107 4a and 5b). Interestingly, the lack of any significant relationship between female  
108 personality and all aspects of pre-breeding pair-bonding is in line with previous  
109 findings showing that male personality is related to various social behaviours  
110 and mating behaviours that female personality is unrelated to<sup>20,26,31</sup>. This may  
111 suggest a general role of male personality in influencing social interactions  
112 across various contexts within this population, which could occur through males'  
113 personality directly shaping their own social behaviour or alternatively through  
114 affecting how others choose to interact with them. Further research into the  
115 extent and mechanisms driving sex differences in the role that personality plays  
116 within this and other systems is now needed.

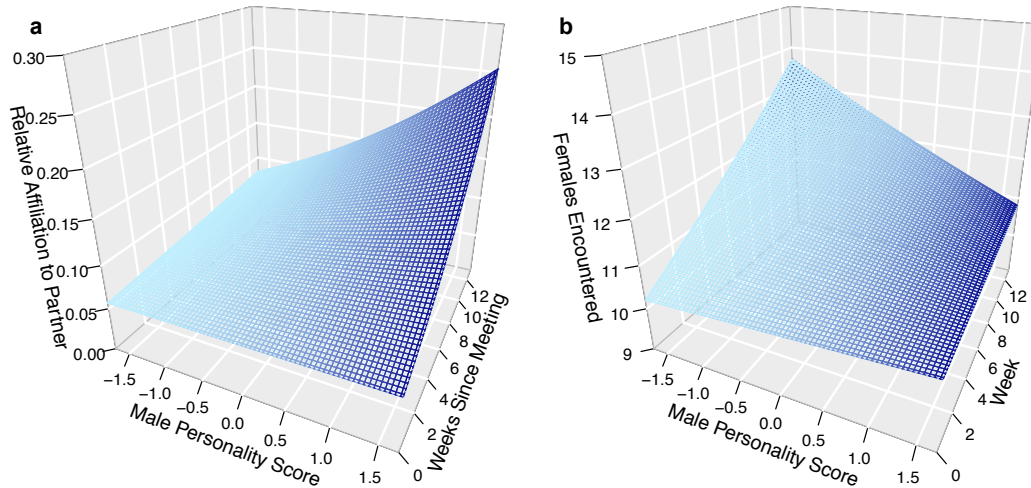
117  
118 In addition to showing that more proactive males form stronger pair bonds  
119 during the pre-breeding period both by meeting their future partners sooner and  
120 increasing their relationship strength at a faster rate, we also examine the  
121 further social consequences of this phenomenon. A strong pair-bond may  
122 potentially provide various future benefits for an individual, such as ensuring  
123 they have a mating partner, potentially allowing earlier breeding or improving  
124 offspring rearing<sup>2,7,13,30,32</sup>, yet efforts to establish and maintain relationships  
125 within any social system are likely to also hold some immediate costs<sup>11,33</sup>. As  
126 such, we found that more reactive (i.e. less proactive) males significantly  
127 increased the number of females encountered each week throughout the winter  
128 in comparison to more proactive males (GLMM with network randomization:  
129 Estimate=-0.006±0.002,  $z=-2.588$ ,  $p=0.010$ ,  $p_{\text{rand}}=0.024$  - Fig. 2b; Supplementary  
130 Figure 6a). Therefore, early partner choice and maintenance of a tighter pair  
131 bond reduced the pool of potential mates sampled. Indeed, it is expected that  
132 prioritising forming a relationship with a particular partner will be traded off

133 against associating with other potential partners in any system where  
134 constraints on social associations exist. In this case, if more proactive males  
135 ultimately mate with 'sub-optimal' partners due to reduced sampling, this may  
136 provide a novel explanation as to why more proactive males are subsequently  
137 more promiscuous during breeding within this population<sup>26</sup>. These differing  
138 social costs (i.e. less mate sampling) and benefits (i.e. stronger pair-bonding) of  
139 proactive males in comparison to reactive males help explain how individual-  
140 level behavioural variation in personality, and pair-bond strength, are  
141 maintained within populations.

142  
143 Given these findings, future work should investigate the precise mechanisms  
144 underlying how individual-level behavioural variation shapes social  
145 relationships across the animal kingdom<sup>5,20,21,34</sup>. This could be considered in  
146 terms of how simple individual differences may manifest as complex social  
147 behavioural patterns<sup>34</sup> as well as how this is shaped by genetic or  
148 neurobiological factors (both of which are known to contribute to personality  
149 and pair-bonding)<sup>8,10</sup>. Furthermore, given that particular individual behavioural  
150 types may be more likely to produce strong dyadic bonds, the potential effect of  
151 population composition (in terms of personality) on the overall architecture of  
152 the social system (i.e. the density of strong dyadic pair-bonds) is of interest,  
153 especially given the consequences of network structure for the functioning of  
154 almost all social processes, such as the spread of information and disease or the  
155 occurrence of cooperation<sup>5,11,21,35,36</sup>.



**Fig 1. | The relationship between individual personality and dyadic pair-bonding.** **a:** An illustrative social network showing the occurrence of pre-mating pair-bonds and in the winter social network. Each node shows an individual bird recorded in the winter 2011-2012 network that subsequently bred (in spring 2012) with an individual also recorded in network. Coloured nodes show those with known personality scores (males = blue, females = green) and the size and shade of the node indicates their position on the reactive-proactive axis (small/light = reactive, large/dark = proactive). Grey nodes are those of unknown personality. The thickness of the connecting lines between the nodes show the strength of the social affiliation between dyads, and affiliations between dyads which subsequently bred together (pair-bonds) are curved and coloured red. See Supplementary Figure 1 for additional network illustration formats. **b,** the relationship between an individual's personality score (reactive to proactive - x axis) and the relative affiliation to their subsequent partner (i.e. their social association strength with their mating partner relative to the sum of all their associations - y axis). Lines show LMM fit (see Methods, and Supplementary Table 2 for full model details) with shaded area denoting standard error (males = blue, females = green). Supplementary Figure 2 considers additional measures of dyadic pair-bonding. **c,** personality score and the week that individuals were first observed with their subsequent breeding partner (0= first observation week of the winter). Lines show GLMM fit (see Methods, and see Supplementary Table 3 for full model details) with shaded area denoting standard error. Supplementary Figure 3 considers additional measures of the time of subsequent breeding partners' first meeting.



**Fig 2. | Personality and temporal patterns in dyadic pair-bonding and encounters.** **a:** 3D surface showing the LMM fit of the interaction between male personality and weeks since meeting their partner on the relative affiliation score i.e. their social association strength with their mating partner relative to the sum of all their associations (see Methods, and Supplementary Table 4 for full model details). Males with higher personality scores (more proactive) have a faster rate of increase in their relative affiliation to subsequent breeding partner over the increasing time since first meeting them. See Supplementary Figure 4a for female personality. **b,** 3D surface showing the GLMM fit of the interaction between male personality and week (since the beginning of winter observations) on the number of females encountered (see Methods, and Supplementary Table 5 for full model details). Males with lower personality scores (more reactive) encountered an increasing number of females each week as the breeding season approaches. See Supplementary Figure 4b for female personality.

## Methods

**Study System.** Wytham Woods, Oxford, UK (51°46'N, 1°20'W) is home to a long-term study population of great tits. The birds form socially monogamous pairs which mostly (>98%) only make one breeding attempt each year that almost exclusively takes place in nestboxes. Egg laying occurs from April onwards and territory prospecting begins 4-6 weeks prior to this<sup>13,37,38</sup>. Successfully provisioning the chicks after hatching requires both parents, and only a small proportion of young (12-13%) are sired by a different father than the provisioning male due to extra-pair matings<sup>26,39</sup>. Since 2007, we have also attached unique RFID-microchips to all captured great tits. The RFID-tags allow the automated recording of the times and locations of individuals' occurrence at sunflower feeding stations (which are equipped with RFID-antennae) as the birds forage in loose aggregations ('fission-fusion' flocks<sup>40,41</sup>) over the winter. A stratified grid of the RFID feeding stations was deployed throughout the woodland covering 65 fixed locations at ~250m intervals through winters beginning 2011, 2012 and 2013. These feeders automatically opened each weekend - Saturday and Sunday - (13 weekends each year from December to March) and scanned for RFID-tagged individuals 16 times per second from pre-dawn until post-dusk.

**Social Networks.** The spatio-temporal datastream of individual RFID detections consists of bursts of activity (as flocks arrive to feed) interspersed by periods of low activity. A machine learning algorithm was used as a robust method to assign each individual record to the flocking event it most likely belonged to<sup>42</sup>. Weighted social networks were then constructed through applying the Simple Ratio Index (SRI) to the 'flocking event-by-individual' matrix<sup>37,40-45</sup> for each year, and also for each separate weekend (Supplementary Methods II). The social associations derived in this way are known to be meaningful, non-random and carry-over to other social contexts and processes within this population<sup>11,20,35,37,40-45</sup>.

**Personality Assays.** Using standard protocols for this species<sup>46</sup>, the Wytham population has undergone personality assays since 2005<sup>20,22,23,26,27</sup>. Wild great tits are taken into separate captive housing and individually assayed for their personality the following morning. The personality score is calculated using a standardized methodology based on each bird's exploration and activity<sup>16</sup> whilst alone in an artificial novel environment. The time of year and number of observations of each bird is also accounted for (see Supplementary Methods III for details). Higher personality scores indicate higher levels activity and exploration, and these birds are classed as 'faster explorers', 'bolder' or more 'proactive' and individual personality (scored in this way) is known to be repeatable, heritable, and biologically and ecologically relevant<sup>18,20,22,23,26,27,31,46</sup>.

## Statistical analysis

### *Personality and pair bond strength.*

We first assessed how each individual's personality predicted the strength of their social network tie to their subsequent breeding partner during the winter pre-breeding period. The primary analysis focused on 'relative partner affiliation strength' (or 'relative pair-bond strength') which was calculated as the social association strength directed towards their mating partner relative to their weighted degree, i.e. the sum of all their associations. This measure ranged from 0 to 1 (where 1 = all their social network associations directed towards their partner). Although this metric was non-symmetric for pairs it was highly correlated between them, so we considered the sexes separately in all of the models throughout the analysis due to this non-independence, and also in line with previous research and findings that personality can be considered separately between the sexes<sup>20,26,31</sup>. Using this individual-based approach, we were able



to estimate the relative pair-bond strength to birds of known personality to their partner regardless of whether their partner (or other birds within the system) also had known personalities.

We ran LMMs which included the personality score as a fixed effect, along with age (adult or first-year), residency status (Wytham born or immigrant), and two key winter observational factors: time (i.e. weekend) of first observation and number of groups/flocking events they were recorded in<sup>43</sup>. Further, the random effects of individual and year ID were included in all models. These factors were consistently controlled for throughout all the analysis. This primary model here set 'relative partner affiliation strength' as the response variable (logit transformed) (Figure 1b; Supplementary Table 2a). However, we also repeated these models but replacing 'relative partner affiliation strength' with (a) pair SRI (a simple measure of pair bond strength) and (b) a measure of bond strength relative to any potential intersexual social association differences (Supplementary Methods IV; Supplementary Figure 2; Supplementary Table 2b & 2c).

As network data is non-independent, we also employed a randomization approach to examine the effect of the variable of interest (personality) on pair bond strength, in line with previous approaches within this system<sup>11,31,37,40,41,43,45</sup>. Through randomly swapping the personality of nodes of the same type (in this case, sex) whilst maintaining the distribution of the data and the relationship of pair bond strength with the other factors in the model, we generated 10000 estimates of the coefficients of the relationship expected between personality and pair-bond under this null hypothesis. By examining where the observed relationship between personality and pair-bond strength fell within this null distribution, we were able to report the significance of the finding ( $p_{\text{rand}}$ ) in comparison to that expected under the same model structures and conditions but when there was no true effect of personality on pair-bond strength (Supplementary Methods IV).

#### *Spatial overlap and time of meeting*

To dissect how individual differences in yearly pre-mating pair strength may arise, we considered spatial and temporal differences in bond formation. Firstly, we examined the extent to which individuals' shared the same spatial range as their future partner. We repeated the same model structure (as above) but set the response variable as individuals' winter spatial range overlap instead of their relative pair-bond strength. Winter spatial overlap<sup>41</sup> was based on how both members of the pair distributed their activity in space and ranged from 0 to 1 (0 = never overlapped and 1 = spatial activity patterns fully overlapped – Supplementary Methods V – Supplementary Table 2d).

Secondly, we considered the time at which a bird first meets its future partner. We defined first meeting as the numerical count of the first sampling period (weekend) in which a pair was first observed in the same flocking event together. We used this measure as the response variable in a zero-inflated negative binomial GLMM (Supplementary Methods V). Again, this model was also consistent with the primary LMM as it included the same random effects and fixed effects (individual characteristic and observational terms) and again considered the sexes separately (Figure 1c; Supplementary Table 3a). We also carried out supplementary analysis (Supplementary Methods V) to verify the results when (a) controlling for any differences in individual gregariousness (Supplementary Figure 3a; Supplementary Table 3b) and when (b) simply considering whether or not the pair was first observed together in their first observational period (Supplementary Figure 3b & 3c; Supplementary Table 3c).

#### *Temporal changes in associations*

We aimed to examine how individual personality related to temporal changes in social associations with their future partner and other individuals as the breeding season drew closer. We created separate, dynamic, social networks for each sampling period throughout the pre-mating period<sup>41,43,45</sup> and calculated the relative affiliation strength to their future partner at each period (Supplementary Methods III & IV). We used these values as the response variable in an LMM which, consistent with the previous models, included the usual fixed effects of age, residency, and number of groups they were observed in (that weekend), but also included an interaction between individual personality and 'weeks since first meeting their partner'. Importantly, this allowed us to examine how the rate of increase in pair-bond strength depended on individual personality (Figure 2a; Supplementary Figure 4a; Supplementary Table 4a). We also carried out supplementary analysis (Supplementary Methods VI) to ensure that any patterns were not driven by differences in general changes in intersexual social associations (Supplementary Figure 5; Supplementary Table 4b).

We also used the weekly networks to examine whether the number of individuals of the opposite sex that they encountered changed over the winter and whether this depended on individual personality. We calculated the number of unique individuals of the opposite sex each individual encountered each week (i.e. their weekly intersexual binary degree), and set this numerical count the response variable in a negative binomial GLMM (Supplementary Methods VI) along with the usual random and fixed factors as well as the week number (i.e. observation period). Importantly, fitting an interaction between week and personality allowed examination of how intersexual encounters through time depended on individual personality (Figure 2b; Supplementary Figure 4b; Supplementary Table 5a). To ensure that any ascribed changes were not due to general changes in degree (rather than intersexual encounters), we also (a) included weekly intrasexual degree as a fixed effect and (b) re-ran the same model but considering weekly intrasexual encounters as the response variable (Supplementary Methods VI; Supplementary Figure 6; Supplementary Table 5b & 5c).

#### **Data Availability**

All data supporting the findings of this study are available with the paper (see supplementary information files)

#### **Ethics**

All work (mist netting, ringing and captivity) was carried out under BTO (A5435) and Natural England licences (20131205 and 20123075), and adhered to UK standard requirements.

#### **Author Contributions**

J.A.F. conceived the study, carried out the analysis and wrote the first draft, J.A.F., E.F.C., C.C.I., J.L.Q. & B.C.S. interpreted the data and planned the draft, J.A.F., E.F.C., L.M.A., A.C., & K.M., collected the data. All authors contributed significantly to revising the manuscript.

#### **Competing interests**

The authors declare no competing interests.

#### **Acknowledgments**

We are particularly grateful to the Social Network Group of the Edward Grey Institute, Oxford University for assistance with fieldwork and help with captive birds, and we thank four anonymous reviewers for their helpful feedback on the manuscript. The work was funded by an EGI Research Fellowship and Merton College JRF to J.A.F and an ERC grant to B.C.S. (AdG 250164). J.L.Q was supported by the ERC (Horizon 2020 FP7/2007-2013 and Consolidator 617509 grants).

365  
366  
367  
368  
369  
370  
371  
372  
373  
374  
375  
376  
377  
378  
379  
380  
381  
382  
383  
384  
385  
386  
387  
388  
389  
390  
391  
392  
393  
394  
395  
396  
397  
398  
399  
400  
401  
402  
403  
404  
405  
406  
407  
408  
409  
410  
411  
412  
413

## References

- [1] Wittenberger, J.F. & Tilson, R.L. (1980). *Annu. Rev. Ecol. Syst.*, 11, 197-232.
- [2] Reichard, U.H. & Boesch, C. (2003). *Cambridge University Press*
- [3] Emlen, S.T. & Oring, L.W. (1977). *Science*, 197, 215-223.
- [4] Lukas, D. & Clutton-Brock, T.H. (2013). *Science*, 341, 526-530.
- [5] Song, Z. & Feldman, M.W. (2013). *J. Evol. Biol.*, 26, 963-970.
- [6] Kleiman, D.G. (1977). *Q. Rev. Biol.*, 52, 39-69.
- [7] Black, J.M. (1996). *Oxford University Press*
- [8] Amadei, E.A. *et al.* (2017). *Nature*, 546, 297-301.
- [9] Young, L.J. & Wang, Z.X. (2004). *Nat. Neurosci.*, 7, 1048-1054.
- [10] Lim, M.M. *et al.* (2004). *Nature*, 429, 754-757.
- [11] Firth, J.A. *et al.* (2015). *Curr. Biol.*, 25, 3138-3143.
- [12] Lack, D. (1968). *Chapman and Hall*
- [13] Perrins, C.M. & Mccleery, R.H. (1985). *Ibis*, 127, 306-315.
- [14] Sanchez-Macouzet, O. *et al.* (2014). *P. Roy. Soc. B-Biol. Sci.*, 281
- [15] Fayet, A.L. *et al.* (2017). *Mar. Ecol. Prog. Ser.*, 569, 243-252.
- [16] Reale, D. *et al.* (2007). *Biol Rev*, 82, 291-318.
- [17] Bengston, S.E. *et al.* (2018). *Nat Ecol Evol*
- [18] Dingemanse, N.J. *et al.* (2002). *Anim. Behav.*, 64, 929-938.
- [19] Sih, A. *et al.* (2004). *Trends Ecol. Evol.*, 19, 372-378.
- [20] Aplin, L.M. *et al.* (2013). *Ecol. Lett.*, 16, 1365-1372.
- [21] Krause, J. *et al.* (2010). *Philos T R Soc B*, 365, 4099-4106.
- [22] Quinn, J.L. *et al.* (2009). *J. Anim. Ecol.*, 78, 1203-1215.
- [23] Quinn, J.L. *et al.* (2012). *P. Roy. Soc. B-Biol. Sci.*, 279, 1919-1926.
- [24] Sih, A. *et al.* (2012). *Ecol. Lett.*, 15, 278-289.
- [25] Dingemanse, N.J. *et al.* (2004). *P. Roy. Soc. B-Biol. Sci.*, 271, 847-852.
- [26] Patrick, S.C. *et al.* (2012). *P. Roy. Soc. B-Biol. Sci.*, 279, 1724-1730.
- [27] Quinn, J.L. *et al.* (2011). *J. Anim. Ecol.*, 80, 918-928.
- [28] Smith, B.R. & Blumstein, D.T. (2008). *Behav. Ecol.*, 19, 448-455.
- [29] Favati, A. *et al.* (2014). *P. Roy. Soc. B-Biol. Sci.*, 281
- [30] Teitelbaum, C.S. *et al.* (2017). *Anim. Behav.*, 134, 147-154.
- [31] Johnson, K.V.A. *et al.* (2017). *Anim. Behav.*, 128, 21-32.
- [32] Gunnarsson, T.G. *et al.* (2004). *Nature*, 431, 646-646.
- [33] Griffith, S.C. *et al.* (2011). *P. Roy. Soc. B-Biol. Sci.*, 278, 2798-2805.
- [34] Firth, J.A. *et al.* (2017). *P. Roy. Soc. B-Biol. Sci.*, 284, 20171939.
- [35] Aplin, L.M. *et al.* (2015). *Nature*, 518, 538-541.
- [36] Allen, B. *et al.* (2017). *Nature*, 544, 227-230.
- [37] Firth, J.A. & Sheldon, B.C. (2015). *P. Roy. Soc. B-Biol. Sci.*, 282, 20142350.
- [38] Firth, J.A. *et al.* (2018). *J. Avian Biol., In Revision.*
- [39] Firth, J.A. *et al.* (2015). *Evolution*, 69, 1336-1344.
- [40] Farine, D.R. *et al.* (2015). *Roy Soc Open Sci*, 2, 150057.
- [41] Firth, J.A. & Sheldon, B.C. (2016). *Ecol. Lett.*, 19, 1324-1332.
- [42] Psorakis, I. *et al.* (2015). *Behav. Ecol. Sociobiol.*, 69, 857-866.
- [43] Aplin, L.M. *et al.* (2015). *Anim. Behav.*, 108, 117-127.
- [44] Firth, J.A. *et al.* (2016). *Biol. Lett.*, 12, 20160144.
- [45] Firth, J.A. *et al.* (2017). *P. Roy. Soc. B-Biol. Sci.*, 284, 20170299.
- [46] Verbeek, M.E.M. *et al.* (1994). *Anim. Behav.*, 48, 1113-1121.



**SUPPLEMENTARY INFORMATION: Personality shapes pair bonding in a wild  
bird social system**

Josh A. Firth<sup>1,2\*</sup>, Ella F. Cole<sup>1</sup>, Christos C. Ioannou<sup>3</sup>, John L. Quinn<sup>4</sup>, Lucy M.  
Aplin<sup>1,5</sup>, Antica Culina<sup>1,6</sup>, Keith McMahon<sup>1</sup>, Ben C. Sheldon<sup>1</sup>

<sup>1</sup>Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS,  
UK

<sup>2</sup>Merton College, Merton Street, University of Oxford, Oxford, OX1 4JD

<sup>3</sup>School of Biological Sciences, University of Bristol, Bristol, BS81TQ

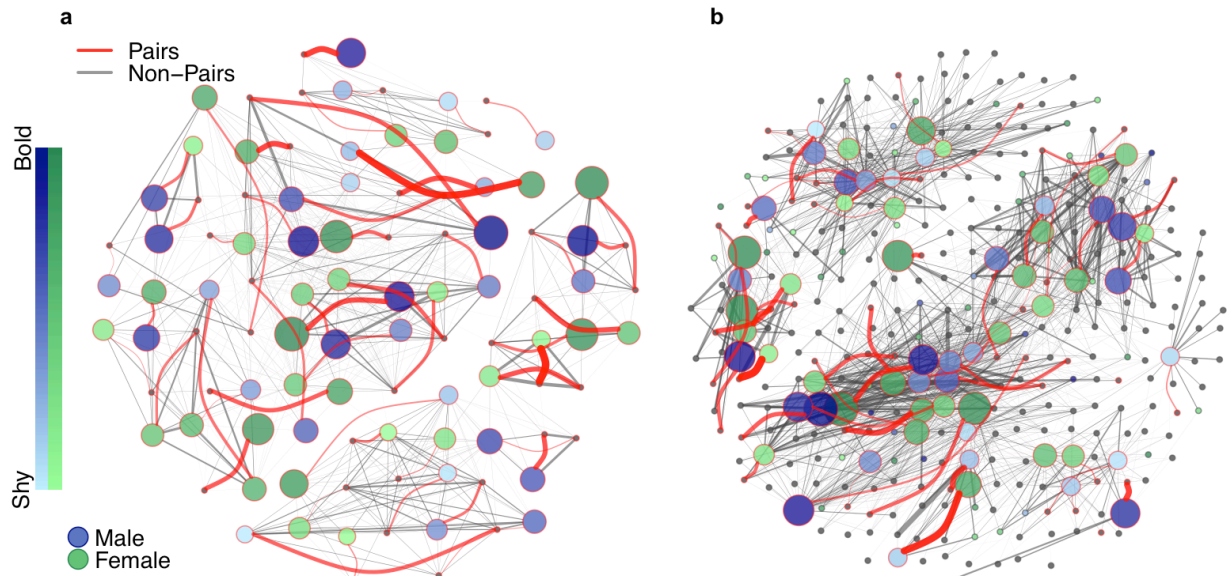
<sup>4</sup>School of Biological, Earth and Environmental Sciences, University College Cork, North  
Mall, Cork, Ireland

<sup>5</sup>Max Planck Institute for Ornithology, Radolfzell, Germany

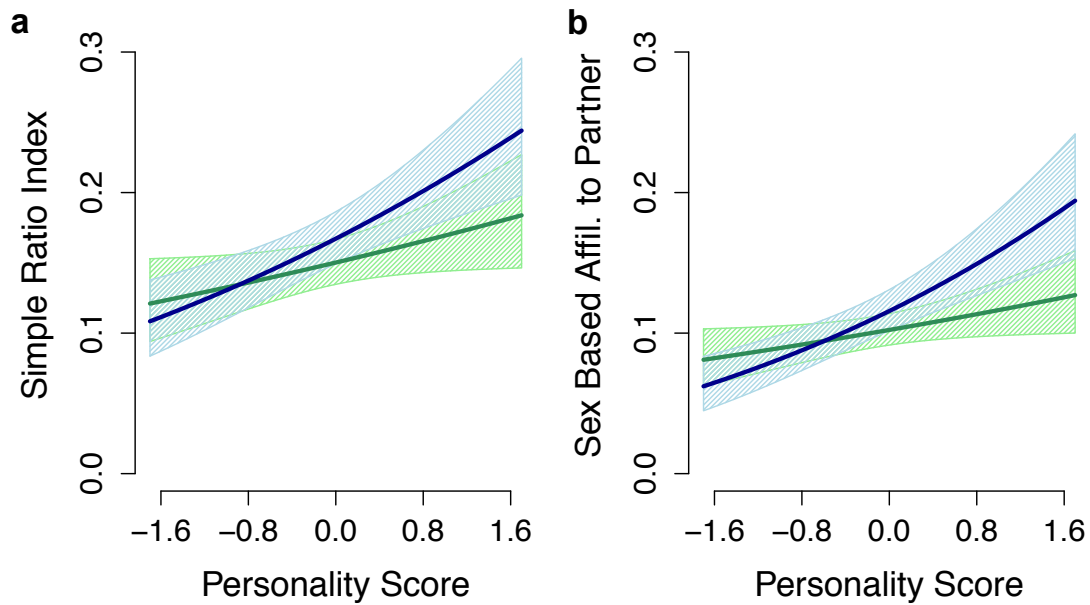
<sup>6</sup>Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, Netherlands

\*Correspondence: Dr. Josh A. Firth [joshua.firth@zoo.ox.ac.uk](mailto:joshua.firth@zoo.ox.ac.uk)

433	<b>Contents</b>
434	1. <b>Supplementary Figure 1.</b> Additional illustrations of the social network
435	showing pair-bonds and personality in winter 2011-2012
436	
437	2. <b>Supplementary Figure 2.</b> Individual personality and additional
438	measures dyadic pair-bonding
439	
440	3. <b>Supplementary Figure 3.</b> Individual personality and additional
441	measures of first meetings
442	
443	4. <b>Supplementary Figure 4.</b> Female personality and temporal patterns in
444	dyadic pair-bonding and male encounters.
445	
446	5. <b>Supplementary Figure 5.</b> Individual personality and temporal patterns
447	in sex-based affiliation
448	
449	6. <b>Supplementary Figure 6.</b> Individual personality and temporal patterns
450	in weighted intersexual social associations
451	
452	7. <b>Supplementary Table 1.</b> Summary of the social network data
453	
454	8. <b>Supplementary Table 2.</b> Pair bonding: model outputs.
455	
456	9. <b>Supplementary Table 3.</b> Time of meeting: model outputs.
457	
458	10. <b>Supplementary Table 4.</b> Temporal rate of pair bonding: model outputs.
459	
460	11. <b>Supplementary Table 5.</b> Temporal encounters with others: model
461	outputs.
462	
463	12. <b>Supplementary Table 6.</b> Additional summary details of models
464	
465	13. <b>Supplementary methods I:</b> additional details of the study system
466	
467	14. <b>Supplementary methods II:</b> additional details of social network
468	inference
469	
470	15. <b>Supplementary methods III:</b> additional details of personality assays
471	
472	16. <b>Supplementary methods IV:</b> additional details of analysis of the effect of
473	personality on pre-mating pair bonding
474	
475	17. <b>Supplementary methods V:</b> additional details of analysis of spatial
476	overlap and time of meeting
477	
478	18. <b>Supplementary methods VI:</b> additional details of analysis of temporal
479	changes in associations
480	
481	19. <b>References</b>

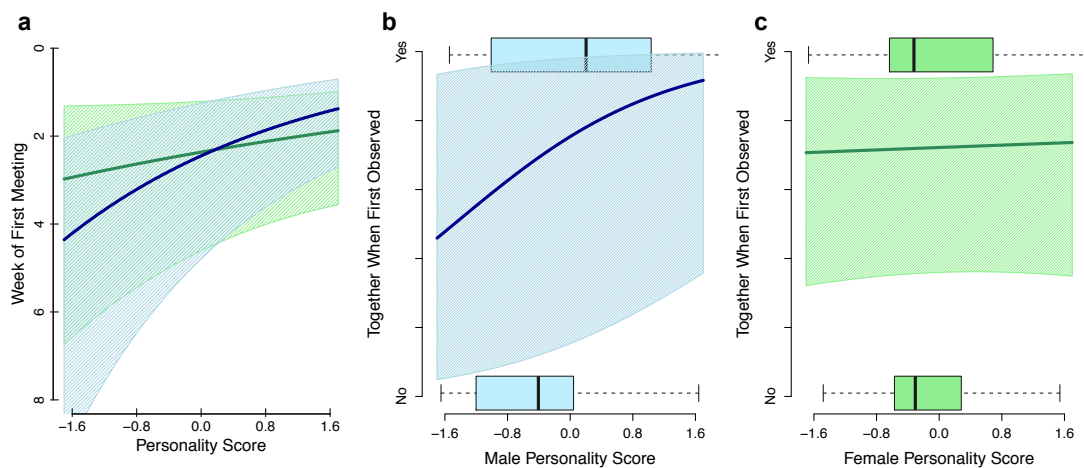


**Supplementary Figure 1. | Additional illustrations of the study system social network.** Follows Fig 1a in main text but uses two variations of illustrating the social network for in winter 2011-2012 in relation pair-bonds and individual personality. Each node shows an individual bird. **Network a** only includes individuals with known personality that subsequently bred with a bird also recorded in the prior winter network whilst **network b** also includes all the associates of these individuals too. Node colour shows sex (males = blue, females = green) and the size and shade of the node indicates their position on the reactive-proactive axis (small/light = reactive, large/dark = proactive). The thickness of the connecting lines between the nodes show the strength of the social affiliation between dyads, and affiliations between dyads which subsequently bred together (pair-bonds) are coloured red.

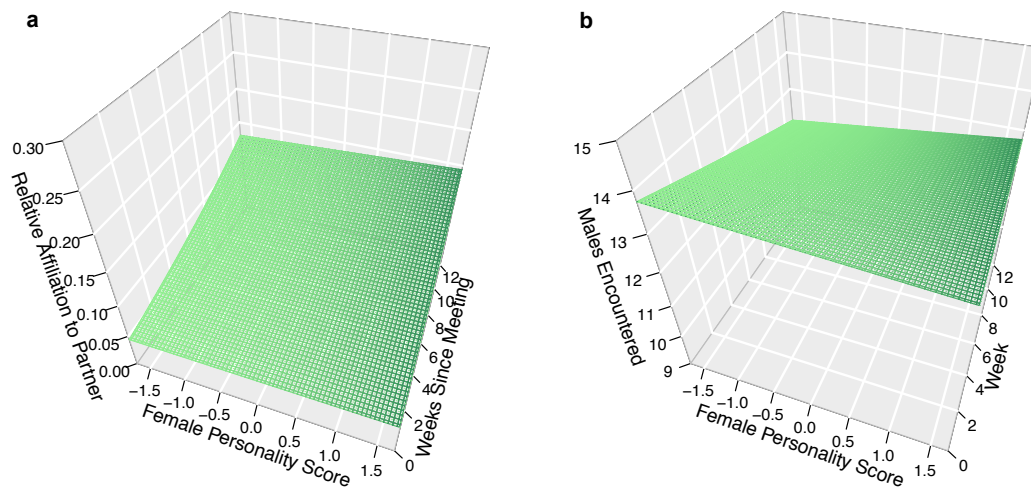


**Supplementary Figure 2. | Individual personality and additional measures dyadic pair-bonding.** Follows Fig 1b in main text but considers variations on the primary measure of relative bond strength (See Supplemental Methods IV). The relationship between individuals' personality score (x axis, reactive to proactive) and their affiliation to their subsequent partner measured as **a**, the simple ratio index (derived directly from the network) and **b**, the sex-based relative association strength (i.e. their pair-bond strength divided by the sum of their weighted associations to individuals of the opposite sex). Lines show LMM fit with shaded area denoting standard error (males = blue, females = green) (Supplementary table 2b & 2c for full model details).





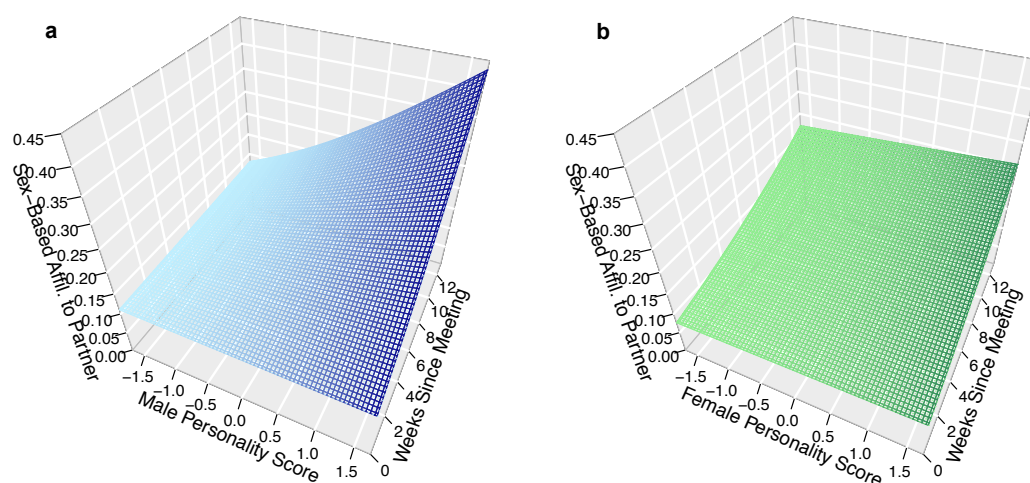
**Supplementary Figure 3. | Individual personality and additional measures of first meetings.** Follows Fig 1C in main text but considers variations on the primary measure of timing of first meeting (See Supplemental Methods V). **a**, personality score and the week that individuals were first observed with their subsequent breeding partner (0= first observation week of the winter). Lines show GLMM fit while controlling for total number of flockmates in week of first meeting (see Methods, and see supplementary tables for full model details) with shaded area denoting standard error. **b**, Male personality score and the probability that the subsequent pair occurred in the same flocking event together in the week in which they were both first observed in the winter prior to mating. Lines show GLMM fit with shaded area denoting standard error (see Supplementary Table 3b & 3c for full model details). Boxplots show the range of male personality scores for those that were with their partner in the first week (top) and those that weren't (bottom). Mid-lines show median, boxes show interquartile range, and whiskers show the range (with values outside 1.5 times IQR excluded). **c**, analogous to Supplementary Figure 2b but considering female personality scores.



546  
547  
548  
549  
550  
551  
552  
553  
554  
555  
556  
557  
558  
559  
560

**Supplementary Figure 4. | Female personality and temporal patterns in dyadic pair-bonding and male encounters.** Follows Fig 2 in main text. **a**, 3D surface showing the LMM fit of the interaction between female personality and weeks since meeting their partner on the relative affiliation score (see Methods, and Supplementary Table 4a). There is an increase in females' affiliation to their subsequent breeding partner over time since first meeting them, but this is unrelated to their personality. **b**, 3D surface showing the GLMM fit of the interaction between female personality and week (since the beginning of winter observations) on the number of males encountered (see Methods, and Supplementary Table 5a). There is slight decrease in the number of males encountered as the breeding season draws closer, but this is unrelated to female personality.

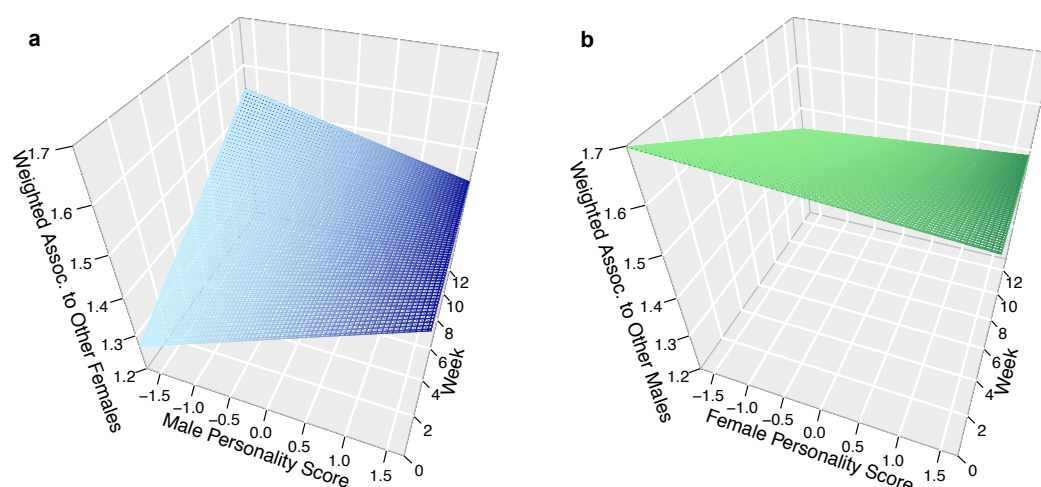
561  
562



563  
564  
565  
566  
567  
568  
569  
570  
571  
572  
573  
574  
575  
576  
577  
578

**Supplementary Figure 5. | Personality and temporal patterns in sex-based affiliation.** **a**, follows Fig 2a in main text. 3D surface showing the LMM fit of the interaction between male personality and weeks since meeting their partner on the sex-based relative affiliation score i.e. their association to their partner divided by their sum of their associations to other females (see Supplementary Methods VI, and Supplementary Tables 4b). Males with higher personality scores have a faster rate of increase in their sex-based affiliation scores to subsequent breeding partner over the increasing time since first meeting them. **b**, analogous to Supplementary Figure 5a but considering female personality scores and female sex-based relative affiliation score i.e. their association to their partner divided by their sum of their associations to other. There is an increase in females' affiliation to their subsequent breeding partner over time since first meeting them, but this is unrelated to their personality.

579  
580



581  
582 **Supplementary Figure 6. | Personality and temporal patterns in weighted**  
583 **social associations to those of the opposite sex. a**, follows Fig 2b in main text.  
584 3D surface showing the GLMM fit of the interaction between male personality  
585 and week (since the beginning of winter observations) on the sum of males'  
586 weighted social associations with other females who they didn't subsequently  
587 breed with i.e. who weren't their mating partner (see Supplementary Methods  
588 VI, and Supplementary Tables 5b for full model details). Males with lower  
589 personality scores held an increasing amount of social associations with females  
590 throughout the winter. **b**, analogous to Supplementary Figure 6a but considering  
591 female personality scores and females' weighted social associations with other  
592 males who they didn't subsequently breed with i.e. who weren't their mating  
593 partner. There is slight decrease in the amount of social associations held with  
594 other males as the breeding season draws closer, but this is unrelated to female  
595 personality.  
596  
597  
598  
599

**Supplementary Table 1. Summary of the social network data.** Summaries are provided for each year (specified in column 1) and each measure (specified column 2) for number of: individuals ('N.inds'), radio-frequency identification detection records ('Records'), occurrences in flocking events ('Flock Occ.') and winter social network connections ('Net Conn.'). The counts are provided for all birds in the pre-breeding network ('All Birds'), breeding birds recorded in the network ('Breederers'), breeding birds recorded in the network mated to a known pair member who was also recorded in the network ('Known PMs'), all birds recorded in the network and with known personality ('PT Birds'), breeding birds recorded in the network and with known personality ('PT Breederers'), and breeding birds recorded in the network and with known personality and mated to a known pair member that was also recorded in the network ('PT KPMs').

Year	Measure	All Birds	Breederers	Known PMs	PT Birds	PT Breederers	PT KPMs
2012/13	N Inds.	1,085	400	240	230	115	62
	Records	2.4mil	1.4mil	645,253	652,072	326,032	183,958
	Flock Occ.	343,458	149,231	91,498	90,365	47,074	26,857
	Net. Conn.	89,904	37,765	22,607	22,989	12,062	6,687
2013/14	N Inds.	720	291	172	134	59	30
	Records	3.2mil	1.5mil	864,237	743,326	333,400	168,813
	Flock Occ.	244,108	114,494	69,386	55,522	26,540	13,762
	Net. Conn.	32,490	14,479	8,961	7,040	3,437	1,852
2014/15	N Inds.	807	257	152	111	45	30
	Records	2.5mil	974,121	636,162	426,431	177,834	126,784
	Flock Occ.	220,678	86,441	56,036	35,605	16,042	11,711
	Net. Conn.	41,806	15,697	9,778	7,109	3,106	2,106
<b>Total</b>	N Inds.	1,833	738	509	290	158	110
	Records	8.1mil	3.5mil	2.1mil	1.8mil	837,266	479,555
	Flock Occ.	808,244	350,166	216,920	181,492	89,656	52,330
	Net. Conn.	164,200	67,941	41,346	37,138	18,605	10,645

**Supplementary Table 2. Pair bonding.** Model outputs of LMM examining the effect of individual's personality, residency status (Wytham born compared to non-wytham born), age (adult compared to first year), the number of groups/flocking events they were observed in and the week of their first observation for their (a) relative pair bond affiliation to their future partner (b) Dyadic simple ratio index with future partner (c) sex-based relative pair bond strength and (d) spatial range overlap with their future partner.

		Male				Female			
Response	Term	Coef	Std.Err	t-val	p-val	Coef	Std.Err	t-val	p-val
(a) Relative bond strength	Intercept	-2.601	0.48	-5.416	<0.001	-2.389	0.287	-8.333	<0.001
	Personality	0.25	0.105	2.373	0.021	0.082	0.09	0.91	0.367
	Res. Status	-0.187	0.221	-0.845	0.402	0.12	0.159	0.754	0.455
	Age	-0.289	0.227	-1.273	0.331	-0.241	0.157	-1.529	0.201
	Groups	0.001	0.001	0.571	0.625	0.001	0.001	-0.236	0.825
	First obs.	0.095	0.062	1.525	0.267	-0.001	0.031	-0.02	0.985
(b) Simple ratio index	Intercept	-1.87	0.54	-3.461	0.001	-2.014	0.403	-4.999	<0.001
	Personality	0.267	0.121	2.205	0.032	0.193	0.121	1.595	0.117
	Res. Status	-0.324	0.255	-1.274	0.208	0.172	0.21	0.818	0.417
	Age	-0.353	0.262	-1.348	0.31	-0.501	0.222	-2.252	0.087
	Groups	0.001	0.001	1.196	0.354	0.001	0.001	1.935	0.125
	First obs.	0.046	0.069	0.663	0.575	-0.026	0.044	-0.602	0.58
(c) Sex-based relative bond strength	Intercept	-2.145	0.577	-3.719	<0.001	-1.797	0.366	-4.916	<0.001
	Personality	0.312	0.127	2.461	0.017	0.12	0.113	1.055	0.297
	Res. Status	-0.193	0.266	-0.725	0.472	0.184	0.199	0.926	0.359
	Age	-0.393	0.273	-1.44	0.287	-0.265	0.201	-1.315	0.259
	Groups	0.001	0.001	0.62	0.598	0	0.001	-0.598	0.582
	First obs.	0.111	0.075	1.494	0.274	0.004	0.04	0.103	0.923
(d) Spatial range overlap	Intercept	0.486	1.106	0.439	0.662	0.496	0.789	0.629	0.532
	Personality	0.334	0.248	1.348	0.183	0.162	0.252	0.643	0.523
	Res. Status	-0.858	0.522	-1.643	0.106	0.483	0.445	1.087	0.282
	Age	-0.652	0.538	-1.211	0.349	-0.809	0.432	-1.873	0.134
	Groups	0.002	0.002	1.086	0.391	0.003	0.001	1.766	0.152
	First obs.	0.139	0.142	0.981	0.430	-0.096	0.086	-1.121	0.325

**Supplementary Table 3. Time of pair meeting.** Model outputs of GLMMs examining the effect of individual's personality, residency status (Wytham born compared to non-Wytham born), age (adult compared to first year), the number of groups/flocking events they were observed in when first meeting their partner and the week of their first observation on (a) the week of the first observation with (i.e. in the same flocking event as) their future partner (b) the week of the first observation with their future partner when also controlling for number of flockmates (degree) at the time of meeting and (c) whether or not they were observed with their future partner in the first week they were both observed in the winter

Response	Term	Male				Female			
		Coef	Std.Err	z-val	p-val	Coef	Std.Err	z-val	p-val
(a) Week of first obs. together	Intercept	-0.073	0.521	-0.14	0.889	0.223	0.405	0.551	0.581
	Personality	-0.368	0.177	-2.076	0.038	-0.105	0.193	-0.542	0.588
	Res. Status	0.795	0.303	2.621	0.009	-0.541	0.324	-1.671	0.095
	Age	0.056	0.492	0.114	0.91	0.919	0.323	2.847	0.004
	Groups	0.015	0.011	1.295	0.195	0.007	0.008	0.807	0.419
	First obs.	0.166	0.054	3.101	0.002	0.165	0.038	4.346	<0.001
(b) Week of first obs. together	Intercept	-0.667	0.55	-1.213	0.225	-0.391	0.541	-0.723	0.47
	Personality	-0.339	0.147	-2.311	0.021	-0.135	0.179	-0.756	0.45
	Res. Status	0.687	0.282	2.439	0.015	-0.551	0.314	-1.759	0.079
	Age	-0.038	0.335	-0.113	0.91	0.971	0.306	3.175	0.001
	Groups	0.016	0.011	1.548	0.122	0.005	0.008	0.603	0.547
	First obs.	0.195	0.048	4.093	<0.001	0.175	0.037	4.742	<0.001
(c) Observed together in first sampling period	Degree	0.017	0.01	1.833	0.067	0.02	0.011	1.897	0.058
	Intercept	-2.63	1.952	-1.347	0.178	0.608	1.105	0.551	0.582
	Personality	0.754	0.377	1.998	0.046	0.043	0.345	0.125	0.9
	Res. Status	-0.822	0.686	-1.198	0.231	0.366	0.593	0.617	0.537
	Age	-1.235	0.944	-1.308	0.191	-0.368	0.611	-0.602	0.547
	Groups	0.007	0.004	1.852	0.064	0.001	0.002	0.463	0.644
	First obs.	0.644	0.321	2.008	0.045	-0.032	0.116	-0.277	0.782

**Supplementary Table 4. Temporal rate of pair bonding.** Model outputs of LMMs examining the week-by-week effect of individual's personality, residency status (Wytham born compared to non-Wytham born), age (adult compared to first year), the number of groups/flocking events they were observed in that week, the weeks since they first met their future partner ('Wks Met') and the interaction of this with individual personality, on their (a) weekly relative pair bond affiliation strength and (b) weekly sex-based relative pair bond strength

		Male				Female			
Response	Term	Coef	Std.Err	t-val	p-val	Coef	Std.Err	t-val	p-val
(a) Weekly relative bond strength	Intercept	-2.008	0.19	-10.57	0.001	-2.334	0.153	-15.279	<0.001
	Personality	-0.013	0.117	-0.107	0.915	0.005	0.098	0.05	0.96
	Weeks Met	0.064	0.01	6.724	<0.001	0.071	0.009	7.545	<0.001
	Res. Status	-0.124	0.212	-0.584	0.591	-0.067	0.143	-0.466	0.658
	Age	0.01	0.228	0.046	0.963	-0.046	0.146	-0.317	0.753
	Groups	-0.011	0.003	-3.583	<0.001	-0.008	0.003	-3.18	0.002
	Pers. x Wks Met	0.026	0.009	2.688	0.007	0.002	0.009	0.203	0.839
(b) Weekly relative bond strength (sex- based)	Intercept	-1.457	0.233	-6.251	<0.001	-1.898	0.187	-10.155	<0.001
	Personality	-0.036	0.143	-0.25	0.803	0.024	0.119	0.197	0.844
	Weeks Met	0.069	0.012	5.985	<0.001	0.083	0.012	7.016	<0.001
	Res. Status	-0.194	0.258	-0.752	0.494	-0.056	0.175	-0.318	0.761
	Age	0.072	0.278	0.258	0.797	-0.015	0.174	-0.087	0.931
	Groups	-0.012	0.004	-3.01	0.003	-0.009	0.003	-2.704	0.007
	Pers. x Wks Met	0.034	0.012	2.934	0.004	0.002	0.012	0.148	0.882



**Supplementary Table 5. Temporal encounters with other individuals.**

Model outputs of (G)LMMs examining the week-by-week effect of individual's personality, residency status (Wytham born compared to non-Wytham born), age (adult compared to first year), the number of groups/flocking events they were observed in that week (scaled and centered), the weeks since the beginning of the winter observations ('Week') and the interaction of this with individual personality, on their (a) weekly intersexual encounters (number of opposite sex individuals encountered that week i.e. intersexual degree) and (b) weekly weighted intersexual social associations (sum of their social associations to opposite sex individuals that week who weren't their future partner i.e. intersexual strength) and (c) weekly intrasexual encounters (i.e. intrasexual degree). Models also controlled for (a) weekly intrasexual degree, (b) weekly intrasexual weighted associations (i.e. intrasexual strength) and (c) intersexual degree, respectively.

		Male				Female			
Response	Term	Coef	Std.Err	z/t-val	p-val	Coef	Std.Err	z/t-val	p-val
(a) Inter-sexual encounters	Intercept	1.518	0.129	11.733	0.001	1.785	0.056	31.923	0.001
	Personality	0.016	0.03	0.548	0.584	-0.009	0.029	-0.304	0.761
	Week	0.012	0.003	4.796	<0.001	-0.007	0.002	-2.959	0.003
	Age	-0.001	0.041	-0.023	0.982	0.003	0.037	0.073	0.942
	Res. Status	0.018	0.05	0.361	0.718	0.028	0.043	0.641	0.521
	Groups	0.001	0.001	1.58	0.114	0.005	0.001	7.475	<0.001
	Intra-degree	0.056	0.001	40.295	<0.001	0.047	0.001	39.464	<0.001
	Pers. x Week	-0.006	0.002	-2.584	0.01	0.002	0.002	0.745	0.456
(b) Inter-sexual weighted associations	Intercept	0.035	0.086	0.409	0.682	0.374	0.07	5.359	0.001
	Personality	0.085	0.056	1.518	0.134	-0.011	0.047	-0.239	0.812
	Week	0.006	0.004	1.535	0.125	-0.017	0.003	-4.85	<0.001
	Age	0.205	0.091	2.247	0.037	-0.143	0.071	-2.015	0.057
	Res. Status	0.02	0.098	0.209	0.835	-0.046	0.073	-0.634	0.528
	Groups	0.002	0.002	1.459	0.145	0.009	0.001	8.47	<0.001
	Intra-strength	0.8	0.026	30.798	<0.001	0.715	0.018	39.381	<0.001
	Pers. x Week	-0.009	0.004	-2.146	0.032	0.002	0.003	0.484	0.629
(c) Intra-sexual encounters	Intercept	1.876	0.05	37.442	0.001	1.548	0.098	15.792	0.001
	Personality	-0.039	0.037	-1.066	0.287	0.001	0.03	0.009	0.993
	Week	-0.004	0.003	-1.365	0.172	0.009	0.002	3.655	<0.001
	Age	0.047	0.041	1.145	0.252	0.055	0.038	1.453	0.146
	Res. Status	0.067	0.065	1.026	0.305	0.037	0.044	0.853	0.394
	Groups	0.086	0.013	6.754	<0.001	0.048	0.011	4.315	<0.001
	Inter-degree	0.043	0.001	34.95	<0.001	0.053	0.001	41.004	<0.001
	Pers. x Week	0.001	0.003	0.108	0.914	0.001	0.002	-0.193	0.847

**Supplementary Table 6. Additional summary details of models.** The table follows the naming of the models used in Tables 2-5. The squared correlation coefficient of the *observed* response value with the *fitted* values obtained from the fixed effects (i.e. not incl. random effects) is given ( $r^2_{[o,f]}$ ) along with the length of the response variable ( $n$ - derived from monitoring the population), the mean of this untransformed response variable, along with its min and max range.

Model	Male					Female				
	$r^2_{[o,f]}$	n	mean	min	max	$r^2_{[o,f]}$	n	mean	min	max
2a	0.141	62	0.085	0.00	0.464	0.103	60	0.066	0.00	0.269
2b	0.081	62	0.199	0.00	0.564	0.039	60	0.182	0.00	0.428
2c	0.149	62	0.149	0.00	0.636	0.114	60	0.124	0.00	0.394
2d	0.106	62	0.724	0.00	1.00	0.218	60	0.713	0.00	1.00
3a	0.28	62	3.452	0.00	13.00	0.408	60	3.717	0.00	13.00
3b	0.332	62	3.452	0.00	13.00	0.446	60	3.717	0.00	13.00
3c	0.244	62	0.677	0.00	1.00	0.024	60	0.717	0.00	1.00
4a	0.077	556	0.127	0.00	0.981	0.093	515	0.098	0.00	0.95
4b	0.066	556	0.209	0.00	1.00	0.078	515	0.165	0.00	1.00
5a	0.796	731	13.895	0.00	53.00	0.754	652	14.546	0.00	40.00
5b	0.586	731	1.427	0.00	5.778	0.683	652	1.559	0.00	5.204
5c	0.742	731	13.581	0.00	43.00	0.807	652	13.405	0.00	43.00

## Supplementary Methods

### Supplementary methods I: additional details of the study system

The great tits in Wytham Woods, Oxford, breed almost exclusively in the nestboxes located in 1020 fixed positions with known GPS coordinates throughout the woodland<sup>1,2</sup>. The provision of the artificial nestboxes allows birds to be trapped as nestlings at age of 15 days as well as trapping the breeding adult pairs between days 6-14 of the nestling phase. All newly captured individuals were fitted with both a metal leg ring from the British Trust for Ornithology (since 1960s) and a plastic leg ring containing a uniquely identifiable Radio-Frequency Identification tags from IB Technology, Aylesbury, U.K (beginning in 2007). Birds were aged (as either 'first-year' or 'adult') and sexed upon capture using either previous breeding records or plumage coloration<sup>3</sup>. As the large majority of breeding birds (>98%) were only recorded at one nestbox in any single year, we excluded the rare occurrences of second breeding attempts throughout the analysis.

Throughout the winter season (September-March), great tits aggregate to form roving feeding flocks<sup>4</sup> that show considerable turn-over as different birds leave and join frequently (high 'fission-fusion' dynamics)<sup>5</sup>. In this period, mist netting at regular intervals targeted birds immigrating into the population, such that the large majority of wintering individuals were RFID-tagged. Previous work<sup>6,7</sup> has estimated that this results in around 90% of the population being tagged.

Each of the 65 RFID feeding station had two access points (on opposite sides of the feeder) fitted with RFID antenna and a datalogging device that scanned for RFID tags 16 times a second and can record a unique RFID tag code up to 3 times per second (Dorset ID, Aalten, Netherlands). Feeders were filled with unhusked sunflower seed on a weekly basis during the non-monitoring periods. As RFID tagged birds landed on the feeding station, their unique 10-digit hexadecimal RFID-tag code, along with the time and location ID for this event, was recorded onto the data-logger. This provides the detailed spatiotemporal information on individual foraging behaviour used throughout the analysis. The RFID antennas operated with high accuracy, and video analysis showed that >99% of all RFID-tagged individual visits to the feeder were recorded correctly<sup>5</sup>. This is similar to the exceptionally low error (i.e. low incorrect reads) and high accuracy (i.e. low proportion of missed reads) rates of RFID recording systems in similar species<sup>8</sup>. The RFID feeders used in this study were fully deployed across three winter seasons: from 03/12/2011 to 26/02/2012, 01/12/2012 to 24/02/2013, and 30/11/2013 to 23/02/2014. Supplementary Table 1 provides a summary of the sample sizes of unique individuals in terms of the number of breeding individuals mated to known partners and those recorded on the RFID feeders over winter.

### Supplementary methods II: additional details of social network inference

As great tits feed in flocks over the winter<sup>4</sup>, the detections of individuals RFID tags at the feeding stations provide a fine-scale, non-uniformly distributed, temporal datastream made up of periods of high activity (bursts) as flocks of

birds arrive and feed together<sup>9,10</sup>. These flocking events can be automatically identified using a machine learning algorithm which employs a Gaussian mixture model (GMM) to detect clusters of visits within each of the temporal data streams at each feeder each day. This method therefore provides a means of avoiding arbitrary or subjective decisions regarding the temporal boundaries of group occurrences, and previous work has shown that determining flocking co-memberships between individuals in this way is more accurate and robust than the current alternatives such as employing set time cut-offs or using sliding time windows of different lengths<sup>10</sup>.

The flocking event co-membership matrices generated from this process are equivalent to 'group-by-individual' matrices, frequently used in animal social network analysis<sup>11-13</sup>. Therefore, the social association between each dyad ( $S_{AB}$ ) was calculated using the Simple Ratio Index (SRI)<sup>14</sup> where

$$S_{AB} = \frac{x}{x+y_{AB}+y_A+y_B}$$

Here,  $x$  denotes the number of flocking event co-memberships between bird  $A$  and bird  $B$ ,  $y_{AB}$  is the number of occasions  $A$  and  $B$  were simultaneously detected apart from one another,  $y_A$  is the number of flocking events that  $A$  occurred in but that  $B$  was not present in, and  $y_B$  is the number of flocking events that  $B$  occurred in but  $A$  was not present in. In this way, the value of  $S_{AB}$  shows the association strength between the dyad where 0 = the dyad was never observed together, and 1 = the dyad always observed together. By calculating  $S_{AB}$  between all dyads for the period of interest, this forms an individual-by-individual association matrix i.e. a 'social network'. Within this context of a network, the 'nodes' denote the identity of the unique birds, whilst the weight of the 'edges' represents the strength of the dyadic link between them. The use of the extensive sampling routines (repeated recording of individuals and co-occurrences) along with these weighted, non-directional, networks, reduces any potential issues which can stem from the 'gambit of the group' approach<sup>13</sup>. The yearly association matrices were derived from pooling the co-occurrence data over all sampling periods over the entire winter (Dec-March), as previous work as suggested that sampling over longer time periods may provide the most accurate inference of social ties<sup>13,15,16</sup>. We also calculated 'weekly' social association matrices calculated from the co-occurrences occurring over each sampling period (weekend) of each winter to allow for the dynamic network analysis<sup>17,18</sup> to assess how social associations and encounters changed over time (see below).

Previous work within this great tit population has shown that social association networks derived using this method are repeatable and consistent, even after accounting for spatial factors or following perturbation<sup>15,16,19</sup> and important to social processes such as the formation of breeding territories<sup>18,19</sup>, the spread of information<sup>20,21</sup> and the gain of new foraging techniques<sup>22,23</sup>. We did not consider relatedness between individuals in any of our analysis, as the network is not kin structured and only ~1-2% of social connections are between first-order relatives<sup>18</sup>.

### **Supplementary methods III: additional details of personality assays**

Mist-nets were used to capture wild great tits through the winter, upon which they were immediately transported to John Krebs Field Station, Wytham, Oxford. Following protocols implemented in this population to measure personality since 2005<sup>24</sup>, birds were kept in indoors, in individual captive housing overnight, and assays began in the morning following capture (between 08.00am to 13.00pm). Personality assays were carried out individually; each bird was released into a novel artificial environment consisting of a plain observational room with five artificial trees (1.5m height, each with four branches). A handheld events recorder (Psion Workabout, Noldus Information Technology, Nottingham, UK)<sup>24-26</sup> was used to record their behaviour and movements over the period of 8 minutes beginning 20s after the bird first entered the room.

Twelve behavioural measures were taken, quantifying various aspects of their behaviour such as the number and duration of flights and hops and the exploration of the area<sup>24,26</sup>. To produce a single personality score for each individual, the square root of PC1 of these measures (which summarises these separately measured, but correlated, behavioural scores well) is used in a LMM which sets individual, as well as time of year and observation number, as factors (see<sup>24</sup> for further details). This also enables a composite score to be calculated for individuals that were assayed on multiple occasions. Scoring behaviour with this approach (or very similar methods) in great tits is one of the longest running measures of personality of wild animals<sup>25</sup>, and has been shown to be highly repeatable and consistent measure, with a heritable genetic component, and predictive of a range of other behaviours both in laboratory settings and the wild in the Wytham population<sup>6,24,26-32</sup> as well in other great tit study systems<sup>25,33-42</sup>.

Following the assays, birds were released back at the site at which they were captured. Recent work has shown that short stays in captivity do not disrupt social structure and individuals generally quickly return to their prior social associations<sup>16</sup>. Supplementary Table 1 summarises the number of birds with known personality that were recorded in the winter social networks and also went on to breed with known partners.

#### **Supplementary methods IV: additional details of analysis of the effect of personality on pre-mating pair bonding.**

The primary analysis set 'relative pair bond strength' as the response variable. However, as is usually the case with social network inference, dyadic association variables can be potentially assessed in various (but often related) ways. Therefore, we also considered two other potential measures of pre-mating pair bonds to ensure the results were consistent and robust across variations in the definition of the dyadic association strength. Firstly, we considered a simple model of pair-bond strength as the direct dyadic value derived from the association matrix i.e. the SRI score (see Supplementary Methods II for details). This represents the most basic measure of pair-bond strength from the network (Supplementary Figure S2a; Supplementary Table 2b). Secondly, we considered a measure additionally aimed at controlling for differences in sex based affiliations. For instance, if a particular type of male was more likely to hold more intersexual social associations, then this may cause this to appear as a difference in pair-bonding too (but in fact just driven by more connections to females in

general). Therefore, we calculated 'sex based relative pair bond strength' as the SRI value to their partner relative to the sum of their weighted social connections (i.e. intersexual weighted degree) to all other birds of the opposite sex. In this way, this measure represents the amount of social associations directed towards their future mating partner given their associations to all others of the opposite sex (Supplementary Figure S2b; Supplementary Table 2c).

The randomisations were carried out for all models considering network data (including those in the supplementary analysis). The aim of the randomisations employed was to generate a null distribution of the relationship between personality and pair-bond strength which could be expected purely under the non-independence and the distribution of the data, and the influence of the other factors on pair-bond strength, but with no actual relationship between personality and pair bond strength. Node randomisations consist of randomly reassigning the labels of the nodes within the network so each individual adopts the identity of another. This approach, in comparison to datastream permutations, has the benefit of maintaining the exact distribution and variance of the dyadic social association scores, and therefore is often favoured when the value of these scores is important to the structure of the model<sup>15,16,19,21</sup> which was the case here due to considering pre-mating pair bonds. In our analyses, as we also wanted to maintain any relationship that existed between pair bond strength and the considered individual characteristics (age and residency status) and observational factors (number of groups and time of first observation), we only reassigned the personality value of the nodes, rather than all of its properties. Further, these reassignments were only carried out between individuals of the same sex (male or female) and breeding status (breeder or non-breeder) and occurring within the same year (or week in the case of the dynamic temporal analysis i.e. Supplementary Methods VI). In this way, each randomization represents a very conservative null model which controls for these factors and maintains the structure of the network but where any relationship between personality and pair bond strength (calculated using the same models as in the observed data) is not truly meaningful. We then carried out this procedure 10000 times, each time running the same model as the primary analysis but replacing the observed personality scores with those generated from one of the 10000 versions of the permuted datasets. By storing each of the new personality coefficients (the effect of personality on the response) from the model, we hence derived the null distribution. Specifically, if the observed estimated effect of personality fell outside the 95% range of this null distribution this indicated a statistically significant effect of personality on pair-bonding, over and above that which could have occurred given the properties of the network and of the model alone. We report the p-value calculated from these randomisations ( $p_{\text{rand}}$ ) calculated as the two-tailed version of the point at which the observed value fell within the null distribution<sup>12</sup>.

#### **Supplementary methods V: additional details of analysis of spatial overlap and time of meeting**

Individual differences in pre-mating pair bond strength could arise through various means. Firstly, we first aimed to examine whether personality related to the overlap in the winter spatial range of a pair. Great tits generally move relatively frequently through the winter<sup>15,18</sup>, but the proportion of time they are active across all sites is not equally distributed between the sites they visit<sup>19</sup>. Therefore, along with the actual spatial range they were recorded within, we also aimed to consider their activity within this range when defining the “winter spatial range overall” of a dyad<sup>18</sup>. Thus, winter spatial overlap for each pair was calculated using a previously published method<sup>18</sup> whereby, firstly, considering each location separately, we calculated the proportion of activity that each pair member spent at each location, and then took the minimum value of the pair at each location, and classified their winter spatial range overlap as the sum of these values over all of the locations. This accounts for both the range they covered as well as how they distributed their activity across these areas e.g. a pre-breeding pair of birds ( $B_1$  &  $B_2$ ) that only were observed at two locations ( $L_1$  and  $L_2$ ), and 95% of  $B_1$  activity was at  $L_1$ , whilst 95% of  $B_2$  activity was at  $L_2$ , would score a winter spatial activity overlap as  $(1-0.95) + (1-0.95) = 0.1$ . If, however, 95% of  $B_1$  activity was instead based at  $L_2$ , the pair would score 1 (i.e.  $0.95 + 0.05$ ). Indeed, the measure ranges from 0 to 1, where, for example, pairs which never visit the same locations as one another would score 0, pairs that – in total – spend half of their activity in the same locations score 0.5, and pairs which spend exactly the same amount of activity at exactly the same locations as one another would score 1. We used these values of individual’s spatial overlap with their partner in a LMM following the primary format used for assessing relative affiliation strength (Supplementary Table 2d).

Along with differences in spatial range overlap, we also considered whether the sampling period in which a bird was first observed in the same flocking event as its future partner was related to its personality. This response variable was zero-inflated, as technically two processes could generate the zero value (i) pairs which actually first met during the first week of observations and (ii) pairs which had met prior to the first week of observations and were then seen together in this first sampling period (weekend) of the winter. The response followed a Poisson distribution, as it was essentially a depleting count of the number of individuals which met their future partner on each weekend. The primary model used a negative binomial error structure that reduces the issue of overdispersion for Poisson model fitting and therefore represents a more conservative approach to estimating significance<sup>43</sup>. However, using a standard Poisson model generally gave the same results (although slightly less conservative) throughout the analysis. This GLMM followed the format of the LMM assessing relative pair bond strength (Supplementary Methods IV) and thus, along with individual personality, also included age, residency, first observation, and number of groups (but over the sampling period they first met rather than the entire year) as fixed effects, and included individual and year ID as random effects (Figure 1c; Supplementary Table 3a). As part of the supplementary analysis, we also wanted to ensure that the effect of personality on time of first meeting was not driven by general differences in gregariousness during that time period. For instance, if an individual was particularly gregarious and engaged in flocking events with lots of individuals, they would be more likely to have engaged in a flocking event with

their future pair member just due to this alone, and therefore more likely to be classed as 'meeting' earlier despite no difference in actual propensity to do so. Therefore, we ran another GLMM but also included the number of flockmates that the individual held in the weekend they were first observed with their future partner (i.e. their 'binary degree' that weekend) as a fixed effect (Supplementary Figure 3a; Supplementary Table 3b). Additionally, to verify the results, we also carried out supplementary analysis to examine whether individual personality was related to the probability that the subsequent pair occurred in the same flocking event together in the week in which they were both first observed in the winter. Here, we used the same primary model structure again, but utilizing a GLMM with a binomial error distribution and considering the response variable as whether or not the pair were observed in a flocking event together during the first period both members were observed (Supplementary Figure 3b & 3c; Supplementary Table 3c).

#### **Supplementary methods VI: additional details of analysis of temporal changes in associations**

Following the methods outlined in Supplementary Methods III, social networks were created for each separate sampling period (weekend) over each of the winters. This gave a total of 49 sampling periods, 8791 instances of unique occurrences of an individual occurring in a weekend network (1071 of these instances were from individuals with known personality that and had already met their known future breeding partners that year).

Firstly, we calculated the relative affiliation strength for each individual that had already met their future mating partner that winter for each weekend as the association score to their partner that weekend in relation to their network weighted degree that weekend (in line with the method for calculating yearly relative affiliation strengths). We then used these (logit transformed) values as the response variable in a LMM which also included the usual variables as well as the number of weeks since they were observed with their partner as a predictor, along with the interaction of this with individual personality. In this way, we were able to examine how the increase in relative affiliation strength depended on both the time since first meeting their partner as well as the personality of the individual (Figure 2a; Supplementary Figure 4a; Supplementary Table 4a). The same format of randomisation tests (Supplementary Methods IV) but only allowing resignments of personality between those observed on the same weekend network (as opposed to year) were employed to examine the significance of the results in comparison to a null model which maintained the same structures of each of the weekly networks, the non-independence of the data, the distribution and variance of the response and the effect of each of the other factors on pair bond strength. Further, we also considered that if personality related to how individuals changed their associations to others of the opposite sex (regardless of whether it was their future mating partner or not) over time, this may cause an apparent relationship between relative affiliation strength and personality despite no additional propensity to increase their actual bond strength with their partner specifically. Therefore, we repeated the analysis but used sex based weekly relative affiliation strength as the response



variable i.e. weekly association to their partner relative to their weekly intersexual weighted degree (Supplementary Figure 5; Supplementary Table 4b) and again including the same factors and additionally testing the results against the randomisation test.

Finally, it may be expected that the amount of social effort dedicated towards a future breeding partner may reduce opportunities to meet other potential breeding partners. Therefore, we used the dynamic weekly networks to calculate each individuals weekly encounters with the opposite sex and set this the response variable in a GLMM (Figure 2b; Supplementary Figure 4b; Supplementary Table 5a) with negative binomial error structure (see Supplementary methods V). As a supplementary analysis, we also calculated the sum of each individual's weighted network associations (intersexual network strength) to those of the opposite sex (apart from to their future mating partner), and used this as the response variable in a LMM (i.e. it functions as a weighted version of the model focusing on number of encounters). Again the usual factors were included along with the interaction between week (since beginning of winter observations) and individual personality. Further, we included their weekly weighted intrasexual degree (sum of all their associations to those of the same sex in that week) as a fixed effect to control for any general changes in association patterns (Supplementary Figure 6; Supplementary Table 5b). In the same way, we directly considered whether personality affected the intrasexual (rather than intersexual) encounters over time through running the negative binomial GLMM but setting the weekly number of encounters with those of the same sex as the response variable (Supplementary Table 6c). For each of the models, the results of interest were again confirmed through comparing them to those generated from the weekly network randomisation test.

## References

- [1] Wilkin, T.A. *et al.* (2006). *J. Anim. Ecol.*, 75, 604-615.
- [2] Wilkin, T.A. *et al.* (2007). *Conserv. Biol.*, 21, 1207-1217.
- [3] Svensson, L. (1992). *British Trust for Ornithology*
- [4] Hinde, R.A. (1952). *Behaviour*, 2, 1-201.
- [5] Farine, D.R. *et al.* (2015). *Roy Soc Open Sci*, 2, 150057.
- [6] Aplin, L.M. *et al.* (2013). *Ecol. Lett.*, 16, 1365-1372.
- [7] Matechou, E. *et al.* (2015). *Ecology*, 96, 1641-1649.
- [8] Schlicht, L. *et al.* (2015). *Behav. Ecol.*, 26, 1404-1413.
- [9] Psorakis, I. *et al.* (2012). *J R Soc Interface*, 9, 3055-3066.
- [10] Psorakis, I. *et al.* (2015). *Behav. Ecol. Sociobiol.*, 69, 857-866.
- [11] Whitehead, H. & Dufault, S. (1999). *Advances in the Study of Behavior, Vol. 28*, 28, 33-74.
- [12] Whitehead, H. (2008). *University of Chicago Press*
- [13] Franks, D.W. *et al.* (2010). *Behav. Ecol. Sociobiol.*, 64, 493-503.
- [14] Cairns, S.J. & Schwager, S.J. (1987). *Anim. Behav.*, 35, 1454-1469.
- [15] Aplin, L.M. *et al.* (2015). *Anim. Behav.*, 108, 117-127.
- [16] Firth, J.A. *et al.* (2017). *P. Roy. Soc. B-Biol. Sci.*, 284, 20170299.
- [17] Blonder, B. *et al.* (2012). *Methods Ecol. Evol.*, 3, 958-972.
- [18] Firth, J.A. & Sheldon, B.C. (2016). *Ecol. Lett.*, 19, 1324-1332.
- [19] Firth, J.A. & Sheldon, B.C. (2015). *P. Roy. Soc. B-Biol. Sci.*, 282, 20142350.
- [20] Aplin, L.M. *et al.* (2012). *P. Roy. Soc. B-Biol. Sci.*, 279, 4199-4205.
- [21] Firth, J.A. *et al.* (2016). *Biol. Lett.*, 12, 20160144.
- [22] Firth, J.A. *et al.* (2015). *Curr. Biol.*, 25, 3138-3143.
- [23] Aplin, L.M. *et al.* (2015). *Nature*, 518, 538-541.
- [24] Quinn, J.L. *et al.* (2009). *J. Anim. Ecol.*, 78, 1203-1215.
- [25] Verbeek, M.E.M. *et al.* (1994). *Anim. Behav.*, 48, 1113-1121.
- [26] Quinn, J.L. *et al.* (2011). *J. Anim. Ecol.*, 80, 918-928.
- [27] Patrick, S.C. *et al.* (2012). *P. Roy. Soc. B-Biol. Sci.*, 279, 1724-1730.
- [28] Cole, E.F. & Quinn, J.L. (2012). *P. Roy. Soc. B-Biol. Sci.*, 279, 1168-1175.
- [29] Quinn, J.L. *et al.* (2012). *P. Roy. Soc. B-Biol. Sci.*, 279, 1919-1926.
- [30] Aplin, L.M. *et al.* (2014). *P. Roy. Soc. B-Biol. Sci.*, 281, 20141016.
- [31] Cole, E.F. & Quinn, J.L. (2014). *Biol. Lett.*, 10, 20140178.
- [32] Johnson, K.V.A. *et al.* (2017). *Anim. Behav.*, 128, 21-32.
- [33] Verbeek, M.E.M. *et al.* (1996). *Behaviour*, 133, 945-963.
- [34] Dingemanse, N.J. *et al.* (2004). *P. Roy. Soc. B-Biol. Sci.*, 271, 847-852.
- [35] Dingemanse, N.J. *et al.* (2002). *Anim. Behav.*, 64, 929-938.
- [36] Drent, P.J. *et al.* (2003). *P. Roy. Soc. B-Biol. Sci.*, 270, 45-51.
- [37] Van Oers, K. *et al.* (2008). *Anim. Behav.*, 76, 555-563.
- [38] van Oers, K. *et al.* (2004). *Behav. Genet.*, 34, 611-619.
- [39] Carere, C. *et al.* (2005). *Anim. Behav.*, 70, 795-805.
- [40] Korsten, P. *et al.* (2010). *Mol. Ecol.*, 19, 832-843.
- [41] Korsten, P. *et al.* (2013). *Nat Commun*, 4, 2362.
- [42] Araya-Ajoy, Y.G. & Dingemanse, N.J. (2017). *J. Anim. Ecol.*, 86, 227-238.
- [43] Hardin, J.W. & Hilbe, J.M. (2007). *Stata Press*